7. TROPICAL RAIN FORESTS AND CORAL REEFS AS OPEN NON-EQUILIBRIUM SYSTEMS

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INTRODUCTION

The great richness of species in tropical communities is well known. But what is often not appreciated is the considerable variation in species richness from site to site within tropical communities. In this paper I will discuss the reason for this variation within particular community types, directing my attention to tropical rain forests and coral reefs, which have usually been regarded as the epitome of complexity, diversity and stability. I suggest that the highly diverse sites in these communities are usually in a non-equilibrium state, in the process of moving towards an equilibrium of lower diversity. In ecological terms, they are in an intermediate stage of a succession towards a low diversity climax, which, in theory, is an equilibrium state of unchanging species composition.

During this process it is important to distinguish between open and closed systems. Caswell's (1978, p. 128) description applied to ecological systems is a useful summary: 'A closed system is one in which the population exists in a single, closed, roughly homogeneous volume of habitat. There is no migration into or out of this single habitat cell. An open system consists, in its simplest form, of a set of habitat cells coupled by migration. The flux of population between cells must be small enough that the cells retain some measure of independence but large enough that the cells are not totally isolated. Notice that an open population system, considered as a whole, may itself be closed. In this sense the distinction between open and closed systems might be described equally well as between subdivided and non-subdivided systems. . . . The most crucial distinction between closed and open systems is that in open systems local extinction is not an absorbing state. Recolonization of a local population that becomes extinct is now a possibility.'

In actual communities, cells are best defined according to the processes that influence the patterns being explained. Thus, in the population models of Andrewartha & Birch (1954) and later workers such as Caswell (1978), the cells are local populations that go extinct and are started again by immigration from

other cells having extant populations. Extended to the community level, local populations of all species may be destroyed on a particular site, with the community being re-established by invasion from the surrounding populations. Here the cell is the empty gap, surrounded by occupied cells. Another definition of a cell uses the viewpoint of a predator that spends most of the time in cells defined by dense clumps of prey, ignoring or passing quickly through cells where prey are sparse. Or if the predator feeds on two species of prey, the predator may feed only in cells of one species, ignoring cells containing the other. In this paper I will use the term cell in all these different ways.

Similarly, the definition of 'equilibrium' depends upon the scale or pattern in which one is interested. In Caswell's (1978) usage, equilibrium applies to events within a cell. For example, if mechanisms exist that keep two competitors co-existing within a cell, the system is in equilibrium; I will use it in this sense in the present paper. However, another acceptable definition is that if two competitors persist indefinitely in an open system of many cells, but in any one cell one species always eliminates the other, the whole system can be regarded as being in 'regional' equilibrium, if the overall species composition does not change. Caswell (1978) has simulated a local open non-equilibrium system of two competitors and one predator and shown that all can persist with reasonable numbers of cells and degrees of migration between them.

I will begin my discussion with cells defined as gaps created by disturbances in forest or coral assemblages. The differences in the adaptations of species that invade earlier vs. later in these gaps were noted in the first studies of succession (Cowles 1899; Cooper 1913). What needs to be emphasized is the fact that once a gap is fully colonized, it is no longer open to further immigration by the 'early' species. This is because some of the adaptations which enable them to invade open sites (e.g. ability to germinate or attach in exposed conditions, high metabolic rates, etc.) make them ill-adapted to invade and survive in the very different conditions existing in occupied sites. Thus, for that particular set of species the system shifts from open to closed to further immigration so that these species then go extinct in that site.

As an example of such changes, consider a forest in which a major disturbance kills all organisms over a large area. The gap represents an empty cell surrounded by occupied cells from which colonists come to invade the empty one. (We assume that the whole area is physically homogeneous and that it remains so throughout the time span under consideration; the role of environmental heterogeneity will be addressed later.) If the area continues to be subjected frequently to major disturbances that create moderate or large-sized gaps (regime I, Table 7.1), the 'early succession' species will continue to invade these openings. The system will be an open non-equilibrium one in which early succession species persist by migrating from cell to cell. In contrast, if there are no more major disturbances for a while (regime II), the smaller gaps that are produced by minor disturbances can no longer be invaded by the early colonists

TABLE 7.1. The sequence during colonization of disturbed sites in a region that is physically homogeneous and without gradual climatic change

Regimes of different scales of disturbance	General classes of species based upon their ability to invade open vs. occupied sites		
	A *Early colonizers* unable to invade occupied sites	B *Intermediates* between early and late colonists	C *Late colonizers* unable to invade open, exposed sites
I. Disturbances moderate to large and frequent	Abundant, dominate cover	(1) *Open non-equilibrium* Less common, subordinate	Absent or rare and near edges of gap
II. Disturbances small and frequent or, if infrequent, at an intermediate time after a large disturbance	(2) *Closed non-equilibrium if disturbances infrequent* Early colonists not replaced die out	(1) *Open non-equilibrium if disturbances frequent* Common, invade in gaps	Common, invade in gaps or shade
III. Disturbances very small and infrequent, or a long time after a large disturbance	(absent)	(2) *Closed non-equilibrium* Intermediate species not replaced die out (absent)	(3) *Open non-equilibrium* or *open equilibrium* Co-existence due to compensatory mechanism (4) *Closed equilibrium* Without mechanisms listed in (3) above, single-species dominance

that require the more open conditions of large gaps. For them the site has become a closed non-equilibrium one and they die out locally (step 2, Table 7.1).

The system will be an open non-equilibrium one for the intermediate and late colonists since small disturbances occur frequently, permitting the inter-mediate-succession species that require small gaps to persist by invading them. (Note that since cells are defined as gaps their size changes with the size of the disturbance.) If, however, gaps are infrequent (regime III), the shorter-lived species among the intermediates will not survive the longer intervals between gaps. For them the system has also become a closed non-equilibrium one, and they die out locally (step 2, Table 7.1).

With very infrequent small disturbances (regime III) only the most shade-tolerant late-succession species will persist, either in an open non-equilibrium or in an open or closed equilibrium. The open systems (step 3, Table 7.1) depend upon the existence of mechanisms that prevent elimination of species. Without these 'compensatory' mechanisms the species best adapted to the prevailing environmental conditions will replace all others in all the cells (step 4), in a closed equilibrium.

What are these compensatory mechanisms that could maintain co-existence in a physically uniform environment? Frequency-dependent mortality, for example switching by generalized predators (Murdoch 1969; Murdoch & Oaten 1975), will do so. It is interesting that where such switching has been found the different prey species are in separate patches, equivalent to different cells in an open system, rather than together in a single cell (op. cit.). The scheme proposed by Janzen (1970) and Connell (1970) for the maintenance of co-existence of tropical rain forest trees is an example of such frequency-dependent predation, in which attack on seeds or seedlings is proportionately heavier in the vicinity of the parent or in dense clumps of seedlings than else-where. Here the cells are quite small, being represented by the area immediately surrounding an adult tree, or by the dense patch of seedlings. As I will discuss later, other forms of mortality besides predation may compensate for the advantage of superior competitive ability.

Another mechanism, termed 'circular networks', was proposed by Jackson & Buss (1975) and Gilpin (1975). Instead of a linear and transitive hierarchy of competing species (species 1 eliminates species 2, 2 eliminates 3, implying 1 eliminates 3), the hierarchy is circular (1 > 2 > 3, but 3 eliminates 1 directly). The mechanism by which 3 eliminates 1 must, of course, differ from that used by 1 and 2 for such a system to work. If all three occur together in a cell, one will win, unless their competitive abilities are exactly balanced, which is unlikely. However, if they occur in pairs in different cells of an open locally non-equilibrium system one member of each pair will go extinct in any one cell, but the whole system will remain in regional equilibrium provided that the balance between rates of dispersal and extinction is the same for all species. Although

the chances of this are small, the rate of competitive elimination may be much slower with circular networks than with linear hierarchies of competitors.

It now seems clear that all of these compensatory mechanisms require a set of cells connected by migration; in other words, an open system. Neither seems to operate effectively within a single cell, a closed system. Without such mechanisms the species best adapted to colonize and survive in cells occupied by its own or other species will increase at the expense of all the other species in the physically homogeneous habitat that we have assumed exists there. Once it replaces all others, the cells will all be occupied by the same species, and migration of identical propagules between cells becomes irrelevant. At that point the system is equivalent to a closed equilibrium of one large cell, since no other species can invade.

Thus, after a single large disturbance, the system progresses as shown in Table 7.1 from steps 1 to 4, from a single large cell through stages with smaller cells (represented by gaps where individuals have died) with some species having become locally extinct because the system has become a closed non-equilibrium for them, to end either in co-existence of several species in an open non-equilibrium or an open equilibrium, or in single-species dominance in a closed equilibrium. During the complete process, therefore, the scale of pattern changes from a large cell to small cells. If there are no compensatory mechanisms, it may eventually return to a large closed cell.

TROPICAL RAIN FOREST TREES

How relevant is this theory to real ecosystems? In a recent paper (Connell 1978) I have addressed the problem of co-existence of many species in two tropical communities. For rain forest trees the evidence suggests strongly that if disturbance seldom occurs, succession will proceed until single-species dominance is achieved. The best evidence comes from the work of Eggeling (1947), who classified different parts of the Budongo forest of Uganda into three stages: colonizing, mixed and climax stands. Using observations made many years apart, he showed that the colonizing forest was spreading into neighbouring grassland. In these colonizing stands the canopy was dominated by a few species (class A in Fig. 7.1), but the juveniles (class B in Fig. 7.1) were of entirely different species. Adults of the class B species occurred elsewhere as canopy trees in mixed stands where a few species dominated (mainly ironwood, *Cynometra alexandrei*, which comprised 75 to 90% of the canopy trees). However, in these stands the understorey was composed mainly of juveniles of the canopy species. Thus, an assemblage of self-replacing species (that is, a climax community of low diversity) had been achieved. This is not a special case; the Budongo forest is the largest rain forest in Uganda and one-quarter of it is dominated by ironwood. Later and more extensive surveys showed that the
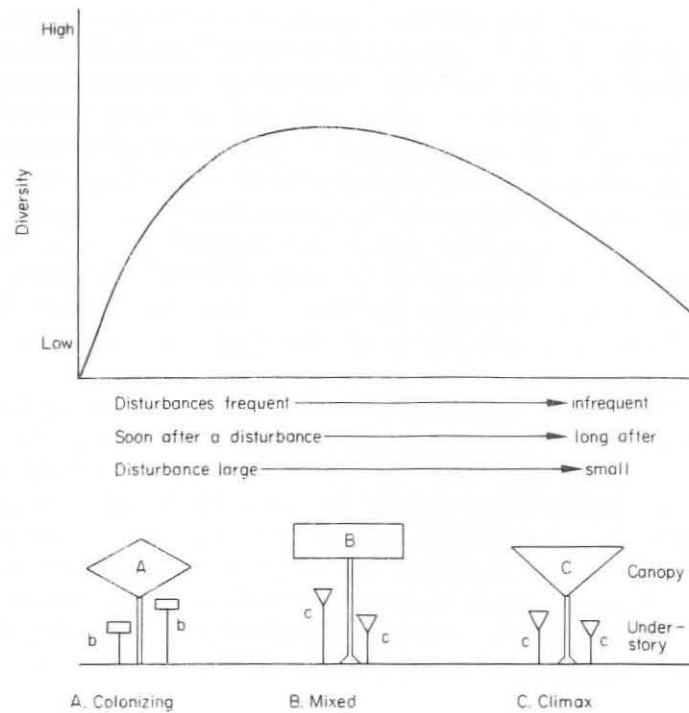
FIG. 7.1. The 'intermediate disturbance' hypothesis. The patterns in species
composition of adults and young proposed by Eggeling (1947) for the different
successional stages of the Budongo forest are shown diagrammatically at the bottom.
(From Connell 1978.)

proportion so dominated in other forests in Uganda is even higher and have
confirmed that, where *Cynometra* dominates the canopy, its juveniles also
dominate the understorey (Langdale-Brown, Osmaston & Wilson 1964).
Extensive stands of rain forests dominated by *Cynometra* or other single species
occur in other areas of Africa, South and Central America and South-East Asia
(Richards 1952; Whitmore 1975).

Another excellent example is the work of Jones (1956) in Nigeria. In this
diverse tropical forest many of the larger trees, aged about 200 years, were
dying. They probably became established in the first half of the eighteenth
century in fields abandoned when the countryside was depopulated by the
collapse of the Benin civilization. These trees had few offspring; most regenera-
tion was by other species, shade-tolerant and of moderate stature. This mixed
forest was, in fact, an 'old secondary' forest that had invaded after agriculture
had stopped, being in about the same state as Eggeling's mixed forest in
Uganda. In both Nigeria and Uganda high diversity was found in a non-
equilibrium intermediate stage in the forest succession.

In most studies of highly diverse stands of tropical rain forests, there exists a set of species having many large trees and few offspring (Richards 1952; Whitmore 1975). Assuming that mortality of juveniles is not directly correlated with abundance, which it was not in two Queensland forests over a period of 9 years as shown in Table 7.2, this means that these species will not replace themselves and will be succeeded by other species that have abundant offspring. Thus, these high diversity forests are in a non-equilibrium intermediate stage in succession after a disturbance.

In a small experimental clearing made in a Queensland rain forest, the pattern of colonization changed in 12 years from an initially rather uniform cover of a few species of early colonists to a patchy mosaic of many different species (Webb, Tracey & Williams 1972). This later subdivision was the result of the properties of the local species, particularly the re-sprouting of survivors of the initial clearing and the proximity of adults that served as sources of seed. Thus, even in the earliest stages of succession, the site was being subdivided into smaller 'cells' by biological activity.

In some instances tropical forests appear to have reached a closed equilibrium state of low diversity. In the climax stands in Budongo with 75 to 90% ironwood in the canopy, there was a great abundance of offspring of ironwood in the understorey. This situation is characteristic of almost all 'single-dominant' forests studied (Richards 1952). However, it is also possible that some mixed high diversity forests might exist as open non-equilibrium systems (step 1, Table 7.1) because small disturbances occur frequently, or as open non-equilibrium or equilibrium systems (step 3) due to the operation of the compensatory mechanisms described above.

I will first discuss the compensatory mechanisms. For example, if the mortality of seeds or seedlings were greater in the vicinity of adults of the same

TABLE 7.2. Mortality of young trees (≥ 0.2 m < 6.1 m tall) in relation to their abundance for two rain forests in Queensland. Not all species had enough young trees to analyse; only those whose adults are capable of reaching the canopy and that had at least six young trees are included. The mortality rate between 1965 and 1974 was plotted against the original numbers mapped in 1965; the least-squares regression slope and correlation coefficient are shown. Neither correlation coefficient is significantly different from zero at $p < 0.05$. (From Connell 1978.)

		Regression of % mortality on abundance	
	Number of species	Slope	r
Tropical, North Queensland, 17°S lat.	49	0·039	0·217
Subtropical, South Queensland, 28°S lat.	46	0·002	0

TABLE 7.3. Mortality of seeds or seedlings near vs. far from adult trees of the same species; all known published field experiments or observations in tropical forests are listed

Location, vegetation type	Plant species	Experimental treatment	% mortality (unless otherwise designated)		Authority
			Near adult	Far from adult	
Queensland, 17°S lat. Evergreen rain forest	*Cryptocarya corrugata*	For each treatment 450 seeds laid on ground in nine half square m plots, 50 seeds/plot. % mortality after 9·5 months:	99·8	99·5	Connell 1970
Same, 28°S lat.	*Eugenia brachyandra*	For each treatment 600 seeds laid on ground in twelve half square m plots, 50 seeds/plot. % germinations in first/second year: Average length of life in months in three cohorts of seedlings during the first year after germination (number at start):	14·8/2·5 4·7 (37) 5·4 (25) 5·7 (27)	14·0/2·3 4·9 (38) 4·0 (22) 3·9 (24)	This paper
Same, 17°S lat.	*Planchonella* sp. nov.	In each treatment (near vs. far) four plots of 2 square m, each having 98 seeds. % mortality of seedlings over 3 years Trenched plots: Untrenched plots:	66, 70 51, 55	14, 27 26, 43	Connell 1970

			Near	Far	
Puerto Rico Evergreen rain forest	*Euterpe globosa*	% non-viable seeds found beneath crown vs. 1·5 to 2·5 m farther away. N for 70/71: near 1 765/1 804; far 337/111	1970: 95 to 100 1971: 0 to 11	83 to 100 0 to 20	Janzen 1972a
Costa Rica, Guanacaste Deciduous forest	*Scheelea rostrata*	% mortality of cleaned palm nuts in piles of 50 in cages. N = near 690, far 681	33·8	35·7	Wilson & Janzen 1972

			Near (≤ 12 m)		Far (13 to 24 m)		
			Line 3	Line 1	Line 3	Line 1	
Same	*Sterculia apetala*	Numbers of herbivorous bugs appearing on seeds placed one per m on lines radiating from parent tree. Number/seed after the following intervals:					Janzen 1972b
		6 (line 3) and 13 (line 1) min:	2·6	6·7	0·3	0·9	
		43 (line 3) and 63 (line 1) min:	5·2	17·2	1·8	3·7	
		213 (line 3) and 228 (line 1) min:	5·9	10·7	10·6	9·0	

Same	*Spondias mombin*	% mortality of seeds found on ground at base of tree vs. under edge of crown of 12 trees (N = 1 200 per treatment)	50	45	Janzen 1975b
Same	*Dioclea megacarpa* (vine)	Observations of % of 22 shoot tips ≤10 m eaten vs. 24 tips > 10 m from adults	86·4	16·7	Janzen 1971

species than elsewhere, or in dense clamps than in isolation, this frequency-dependent mortality would constitute an open non-equilibrium system promoting co-existence of many species (Janzen 1970; Connell 1970). However, the evidence concerning this mechanism is equivocal. As shown in Table 7.3, a series of experiments and observations have indicated that mortality of tropical forest seeds and seedlings can be either greater, equal or lower near adults of their own species than elsewhere. Table 7.4 indicates also that increased density may or may not increase mortality. The seed experiments in Tables 7.3 and 7.4 were necessarily all done on species with large seeds, often the shade-tolerant 'climax' species. Comparisons of all species in two forests (Table 7.2) showed no correlation of mortality with abundance. However, an analysis I had made (Connell 1970, Table 7.3) showed that tree seedlings and saplings occurring in single-species clumps (i.e. those having nearest neighbours of the same species) suffered greater mortality than those occurring intermingled with other species.

Since in the same forest some species show frequency-dependent compensatory mortality and some do not, this cannot produce an equilibrium state. Species in which the mortality of seedlings is less or equal nearer than farther from the parent will have an advantage over others with the same dispersal

TABLE 7.4. Effect of density on mortality of seeds; the *Cryptocarya* and *Scheelea* seeds were placed far from adults of the same species. All published observations and experiments known from tropical forests are included

Location, vegetation type	Plant species	Experimental treatment	% mortality		Authority
			Dense	Sparse	
Queensland, Australia Evergreen rain forest 17°S lat.	*Cryptocarya corrugata*	50 seeds in each of nine ½-m plots vs. a seed every meter along a line 104 m long. Mortality after 9·5 months	100	99	Connell 1970
Costa Rica, Guanacaste Deciduous forest	*Acacia farnesiana*	% mortality of seeds on ground in dense stand of trees vs. in stand with trees sparse, intermixed with other species. N = 36 trees from dense stand, 11 from sparse stand, 30 to 100 pods per tree examined, 8 to 10 seeds per pod	79·7	79·6	Janzen 1975b
Same	*Scheelea rostrata*	Piles of 50 (in cages) vs. isolated pairs of cleaned nuts placed above litter. N: dense, 681; sparse, 82	35·7	6·1	Wilson & Janzen 1972

capacity but in which the mortality of seedlings is greater near the parent. In summary, the evidence indicates that this form of compensatory mechanism is apparently not effective in maintaining high diversity in the tropical forests studied.

The original hypothesis (Janzen 1970; Connell 1970) invoked herbivores as the agents most likely to be responsible for higher mortality of seedlings in denser clumps or nearer adults of the same species. Since herbivorous bugs did discover seeds more quickly if they were placed nearer the adults than farther away (Table 7.3, *Sterculia* during the first hour only), and since shoot tips of seedlings were much more heavily eaten closer to adults (Table 7.3, *Dioclea*), this seems a reasonable mechanism. Yet, except for leaf-cutter ants, herbivores are seldom commonly observed in tropical rain forests (Elton 1973). However, this does not signify that their effects are slight, since damage may be difficult to detect (especially that caused by small animals and micro-organisms, or by sucking insects above ground) and may occur sporadically in time and space. Nevertheless, the results of the experiments and observations shown in Tables 7.3 and 7.4 indicate that herbivores are not generally effective in the manner proposed in the original hypothesis. Only one species (*Planchonella*) of the six in which mortality was estimated (Table 7.3) had greater mortality nearer adults than farther away. Also, only one of the three species in Table 7.4 had greater mortality at higher densities.

There are several possible reasons why herbivores are not effective in this way. First, it requires a high degree of specialization. Herbivores must choose to attack seeds or seedlings of a certain species proportionately more strongly near adults of the same species, ignoring all other juveniles. Although it has been shown that herbivorous insects in the tropics are more specialized on particular families of plants (Scriber 1973), species-specificity of tropical herbivores has rarely been unequivocally demonstrated. To do so would require that large samples of all possible species of host plants in a local area be examined in detail. The less complete the survey, the more specialized the herbivores will appear to be. While exhaustive surveys have been done in the temperate zone, notably by the Canadian Forest Insect Survey (Watt 1964), I know of no published evidence from tropical forests that even approaches this degree of completeness. Thus, tropical data will tend to indicate greater specialization due to inadequacy of sampling. The only exception may be that of Janzen (1975a), although no data have yet been published to indicate whether the sampling of the plant species was adequate. He states (op. cit., p. 42) 'of 111 species of bruchid beetles collected to date breeding in seeds of Costa Rican deciduous forest tree seeds, each of 102 of them seems to have only one host plant and each is different from that of the others.' He goes on to point out that general surveys of herbivore diets may be misleading because, although a species may have different hosts in different regions, it still may be species-specific in any one locality. In summary, until some evidence is published, I must conclude

that tropical herbivores have not been shown to be sufficiently specialized to produce the degree of compensatory mortality needed for this mechanism to apply generally.

Secondly, deleterious effects of herbivores on plants are undoubtedly reduced by the attacks of their predators, parasitoids, parasites and pathogens, and by the chemical and mechanical defences of the plants. As indicated in Figure 7.2, there are several links in the food web of animals in forests, such that the effects of natural enemies may either increase or decrease the deleterious effects of herbivores. As Lawton & McNeill (1979) have pointed out, natural enemies probably cannot control the abundance of herbivorous insects if the latter have very high rates of natural increase. They suggest, however, that if these rates are reduced by the defences of the plants themselves, the natural enemies will have a much greater chance of controlling the numbers of herbivores. It seems that the combined forces of plant defences plus natural enemies have been enough to reduce the effects of herbivores on many of the young trees in the tropical forests studied. Thus, herbivores have apparently not been effective in maintaining species diversity of tropical forest trees in the manner suggested by Janzen (1970) and Connell (1970).

Circular networks are less likely in organisms as similar as trees in a forest stand. As described above, a very different competitive mechanism must operate for at least one of the links in a circular network. Consequently, the
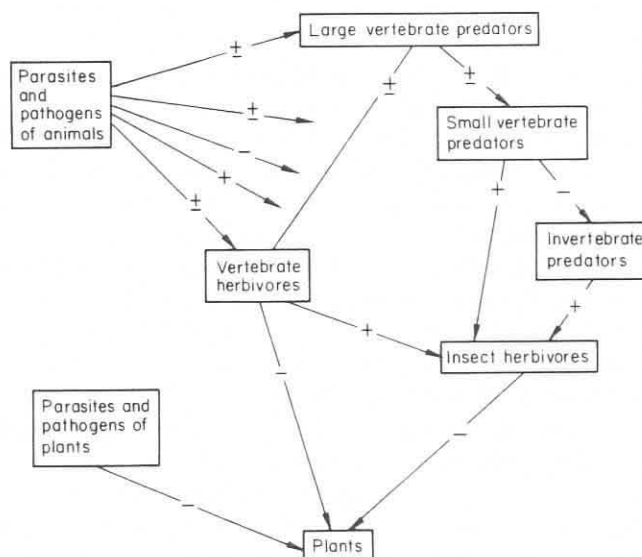

FIG. 7.2. Effects of other organisms on plants in a forest. The sign (+/−) on each arrow indicates the eventual effect of that interaction on plants. Thus, a predator that ate an insect herbivore would have a positive effect on the plant.

likelihood of a sufficiently different mechanism would be increased if the proponents were themselves very different (Jackson & Buss 1975). In their original examples, the organisms exhibiting circular networks were sessile marine invertebrates in different phyla. Since plants compete for light, soil nutrients and water and may interfere with each other using allelopathic chemicals, this mechanism remains a possibility.

Thus, compensatory mechanisms have not yet been found which could be effective in maintaining an equilibrium system in the absence of disturbance as shown by step 3, Table 7.1. Unless some such mechanisms do operate, diversity should decrease as shown in step 4, unless small disturbances occur frequently enough (step 1). Then the forest as a whole will be an open, locally non-equilibrium system of empty and filled cells which might achieve a regional equilibrium ensuring persistence of certain less shade-tolerant species among the more tolerant ones (Grubb 1977).

In summary, the highest diversity of tropical rain forest trees should occur either at an intermediate stage in succession after a large disturbance or with smaller disturbances that are neither very frequent nor very infrequent; either represents an open non-equilibrium. I have called this the 'intermediate disturbance' hypothesis (Connell 1978) and it is illustrated in Figure 7.1. With frequent large disturbances or soon after a single large disturbance, diversity will be low because only a few species have evolved the adaptations necessary for rapid colonization of such exposed, open sites. At an intermediate interval after a large disturbance, diversity should be high because many more species have had a chance to become established before the disappearance of the first invaders. If disturbances are frequent but small, diversity should also be high because species that are either moderately or very shade-tolerant (B and C types, Table 7.1) will co-exist. Eventually, if disturbances are both very small and infrequent, diversity will be lower, as the species which cannot become established in heavy shade or small light gaps will go extinct locally. The level of diversity will then depend upon the degree to which the compensatory mechanisms described above act (steps 3 vs. 4, Table 7.1).

Since the evidence so far indicates that such compensatory mechanisms are not generally effective in tropical forests, the high diversity often observed is more likely to be a consequence of the forest having an intermediate regime of disturbances, as indicated by II in Table 7.1. This represents an open, locally non-equilibrium system that may or may not be in regional equilibrium. If disturbances are frequent enough so that empty cells are formed at a sufficiently high rate to match the survival and seed dispersal rates of the less shade-tolerant intermediate species (class B, Table 7.1), then the forest is in regional equilibrium. Yet in most high diversity mixed rain forests there exists a set of species of large canopy trees which have few or no offspring within the forest, though they occur in permanently open sites along nearby roads (Richards 1952; Whitmore 1975). This indicates that they probably require very large openings

to become established, so are members of class A in Table 7.1. These long-lived species apparently exist in an open, locally non-equilibrium system which requires occasional large disturbances to maintain their presence in regional equilibrium.

REEF-BUILDING CORALS

Corals share many of the characteristics of terrestrial woody vegetation: most of their energy comes from photosynthesis of contained zooxanthellae, they are long-lived and have the same reiterated modular body pattern (Harper 1978). In form corals resemble bushes rather than trees. As in shrub stands, there is little understorey beneath corals. They spread laterally, interacting with neighbours at the borders and often becoming detached into separate portions as do shrub clones.

The relationship between disturbance and species richness is similar in corals to that in tropical forests. In my studies at Heron Island, Queensland, I found the greatest species densities in places either with fairly frequent disturbance by storms or near the surface on reef crests where desiccation at low tide occasionally caused local mortality. In the 15 years I have been studying this reef, three hurricanes have struck it, each causing different degrees of damage to the same permanently marked quadrats. One small region, subtidal and protected from storm waves by an adjacent reef, has escaped all damage and, though almost completely covered with living coral, has low species diversity.

In following the population dynamics of corals on particular sites (by photographing them at intervals), I have found (Connell 1973, 1976, 1978) that where storm damage is frequent they remain as open non-equilibrium systems (Fig. 7.3A), corresponding to regime I in Table 7.1. However, in the region protected from storm disturbance, the coral cover was mainly 'staghorn thickets', consisting of a few huge colonies of branching *Acropora* species that have overgrown all smaller neighbours. Judging from their size (up to 6 m in diameter), they are probably at least a century old (after the initial years of life most corals have rather constant growth rates, so age can be estimated with fair confidence; Connell 1973, Table III). Thus, they had not been seriously disturbed for at least a century, and possibly much longer. Since this area has also served for many years as a protected anchorage for small boats, there is a certain amount of small-scale damage from anchors, with the result that colonies of other species occur, having recently colonized these gaps. This region is thus an open non-equilibrium system, due to the continual provision of small gaps which may be invaded by corals of lesser competitive ability than staghorns (regime II, Table 7.1).

A few species of corals seems to fit into the class A of Table 7.1, 'early colonizers'. These are *Pocillopora damicornis*, *Porites* spp., *Cyphastrea microphthalma*, *Leptastrea purpurea* and *Acropora palifera*. The first three were the
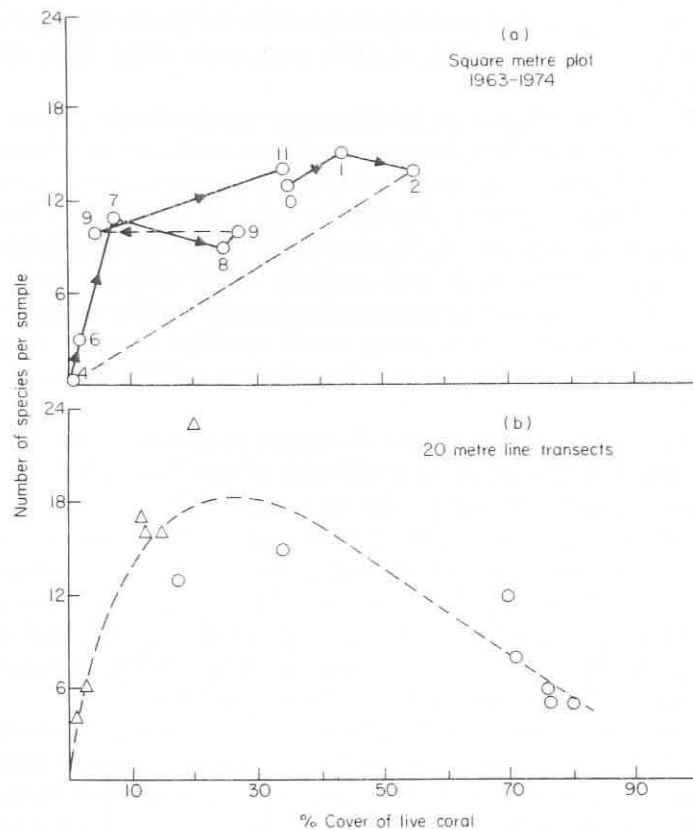
FIG. 7.3. Species diversity of corals in the subtidal outer reef slopes at Heron Island, Queensland. (a) Changes over 11 years on one of the permanently marked plots on the north slope. The number at each point gives the years since the first census at year 0 (no censuses were made in years 3, 5 and 10). The dashed lines indicate changes caused by hurricanes in 1967 and 1972. (b) Results from line transects done 3 to 4 months after the 1972 hurricane. △, data from the heavily damaged north slopes; ○, data from the undamaged south slope; the line was drawn by eye. Where disturbances had either great or little effect (very low or high per cent cover respectively) there were few species, with maximum numbers of species at intermediate levels of disturbance. (From Connell 1978.)

only identifiable corals that colonized artificial surfaces over 11 months at Low Isles, Queensland (Stephenson & Stephenson 1933). On concrete surfaces on the reef flat at Heron Island, I found only the species of *Pocillopora* and *Acropora* listed, even after four years' exposure. In the undisturbed site of low diversity, only one of these species occurred on four line transects of 20 m each that were dominated by staghorn corals; it consisted of a single, very large, old

colony of *Porites* sp. that towered above the staghorns around it. In the gaps other 'intermediate' species of lesser competitive ability than staghorns had colonized.

From this evidence I suggest that these undisturbed areas covered by a few species of competitively dominant staghorn corals are closed to invasion by these 'early colonizing' species of Table 7.1 but open to 'intermediate-stage' species. These sites have reached the stage of regime II of Table 7.1 and are now in an open non-equilibrium state, due to the occasional small-scale disturbances from small boat anchors. Their diversity is generally low (Fig. 7.3b) because the disturbances are few and small, and because staghorns are well adapted to colonizing small openings because fallen branches very quickly become attached to the substratum (observations by myself and R. Day).

Do compensatory mechanisms operate to maintain diversity of corals in the open non-equilibrium or equilibrium of step 3 in Table 7.1? In regard to circular networks, I found none in a study of interactions between corals (12 species, 55 colonies, 82 interactions observed over 9 years; Connell 1976). As in trees, corals may be too similar for such circular networks to occur commonly. Frequency-dependent mortality remains a possibility. Although predation by the starfish *Acanthaster planci* is often intense, evidence indicates that it acts in a reverse frequency-dependent way, attacking preferentially the rare species (Branham *et al.* 1971; Glynn 1974, 1976).

However, the physical environment can act in a way that compensates for the competitive advantage enjoyed by some species such as staghorn corals. I measured the mortality of corals over a 4-year period that included a hurricane at Heron Island in Queensland. As described above, I had ranked these species in competitive ability by observing dynamic interactions over a period of 9 years on permanent quadrats. On the part of the reef crest that was badly damaged by the hurricane, the mortality of those species of corals that ranked high in the competitive hierarchy was much greater than those ranked low (Table 7.5). In contrast, the high-ranked species on an undamaged part of the reef crest had a lower mortality than low-ranked species over the same period. The reason for the difference was that the long-branched form of the superior competitors, the staghorns, made them more susceptible than inferior competitors to being broken off in storms. I have also found (Connell 1973) that branching species are more susceptible to being attacked by boring molluscs and sponges, increasing their vulnerability to damage in storms. Thus, species of corals that ordinarily win in competition suffer proportionately more from storm damage, compensating for their advantage.

Another instance in which the physical environment acted in a compensatory way to promote co-existence was also observed on the reef crests at Heron Island. As the larger branching colonies grow, they spread horizontally, eliminating their neighbours. However, they also grow upwards, and since

TABLE 7.5. Changes in coverage of corals of different competitive abilities. In each area two square metres were censused. (From Connell 1976.)

| Degree of vulnerability to storm damage | Species whose competitive abilities are | | | |
| | High (branching *Acropora* spp.) | | Low (encrusting spp., massive spp., *Pocillopora, Stylophora*) | |
	Cover (cm²) in 1965	% change in cover, 1965–69	Cover (cm²) in 1965	% change in cover, 1965–69
High (north crest)	10 655	− 39·1	3 071	+ 18·6
Low (south crest)	7 027	+ 47·3	1 900	− 12·5

these crests are very shallow, the highest parts of the colony, usually near the middle, are killed by desiccation in the air. These dead portions are then eroded down by boring organisms, so that they become suitable for colonization by new colonies. Thus, the fast-growing superior competitors, although they eliminate other species, cannot monopolize the space on these shallow crests. Consequently, diversity remains high there even though much of the space is occupied (see Plate 2).

In summary, on the reef at Heron Island I found sites with each of the disturbance regimes of Table 7.1. Hurricanes have been frequent and each of the three that occurred during the 15 years of my study caused different patterns of damage. In areas unprotected from hurricane damage, the system resembles an open non-equilibrium system maintained by large disturbances (regime I). In contrast, in a site that had been protected from hurricanes for a long time by an adjacent reef, most of the area was covered by large colonies of 'staghorn' corals, with small openings presumably caused by boat anchors. This site was, therefore, in regime II, most early colonists having been eliminated (step 2) and the intermediates persisting by invasion of the small openings in an open non-equilibrium. Thirdly, on certain portions of the reef crest, the fast-growing superior competitors suffer more mortality than the inferior ones, due to the desiccation or breakage described above. Since the disturbances are minor (regime III) and the mortality compensates for the competitive advantage of some species even when the colonies are closely intermingled (see Plate 2), this is the open equilibrium described in step 3. Finally, one would predict that in the subtidal where there is no desiccation stress and without small disturbances, the system would not be in open equilibrium. Since there apparently were no circular networks or frequency-dependent mortality, the species of staghorn most effective in competition should then eliminate all other species and the system would go to step 4, a closed equilibrium.

THE ROLE OF ENVIRONMENTAL HETEROGENEITY

Up to this point we have assumed that the physical environment was homogeneous in space and time. If so, diversity could be high only under a regime of intermediate-scale disturbances, unless some compensatory mechanisms were operating as described. Even without these factors, if the environment were heterogeneous within a local site or if the climate were gradually changing, species adapted to these differences would co-exist (Connell 1978).

The problem is to estimate the relative contributions towards the maintenance of diversity of environmental heterogeneity vs. disturbance and compensatory mortality. Environmental heterogeneity obviously exists and, with enough imagination, can be used to account for all diversity. No matter how diverse the assemblage, co-existence at equilibrium of many species requires only that each be sufficiently specialized to slight differences in the environment. For example, adaptations of tropical trees to slight differences in soil topography were invoked by Cain (1969) to explain the co-existence of many species of trees in tropical rain forests.

However, in my opinion, it is impossible to test such a hypothesis. First, it would be extremely difficult to decide with any certainty whether the species were, in fact, specialized to the required degree. Secondly, it would be impossible to be sure that one had chosen the relevant 'niche axes' to study. For example, even if it were demonstrated that the heterogeneity of the soil was no greater in a high diversity site than in one dominated by a single species (as in Eggeling's (1947) studies in Uganda), the objection could still be made that perhaps the soil characteristics that were measured were not the ones to which the species were adapting.

Specificity to particular habitats in tropical trees and corals exists but is extremely unlikely to be narrow enough to permit 100 species of trees to co-


PLATE 2 (facing).   Interactions between corals in the same area over 8 years on the north crest, Heron Island, Queensland. For each photograph the square metre frame, divided into 20 × 20 cm squares, was positioned on the permanent stakes visible on the right-hand side; it was removed between times.

Notice the expansion of the platform coral that was centred in C–2 in 1963. There was a 'stand-off' between it and its neighbour of another species in C–1 for the entire 8-year period. In contrast, over the first 6 years it expanded rapidly into squares A–2, B–2 and B–3, covering colonies of both soft and hard corals. There was also a stand-off for 2 years with its neighbour in C–3, then after some damage from a hurricane in January 1967 a rapid expansion over that neighbour into C–4. In A–3 it was stopped by the massive coral in 1969 and was dying back in 1971, owing to the fact that the massive coral had digested off the tissues of the growing tips, so preventing overgrowth. Lastly, notice the death of the central oldest portion in C–2 in 1969 and partial regrowth in 1971. In 1972 another hurricane killed all the corals on and surrounding this site, except for a small portion of the massive one in A–3.
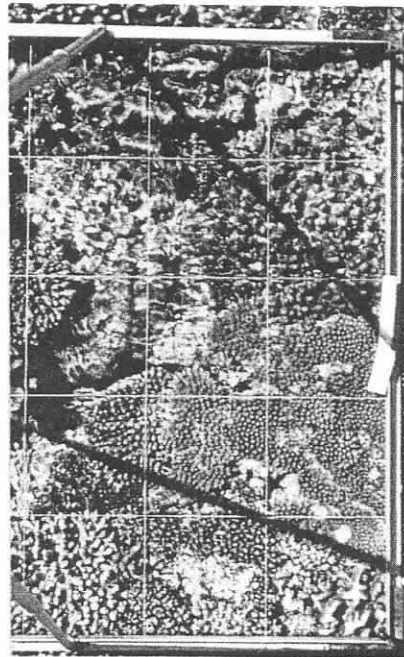
(The photographs were taken in October 1963 and in August of the other three years.)
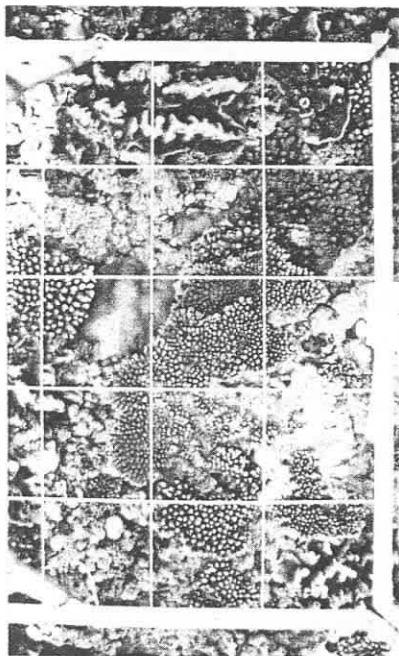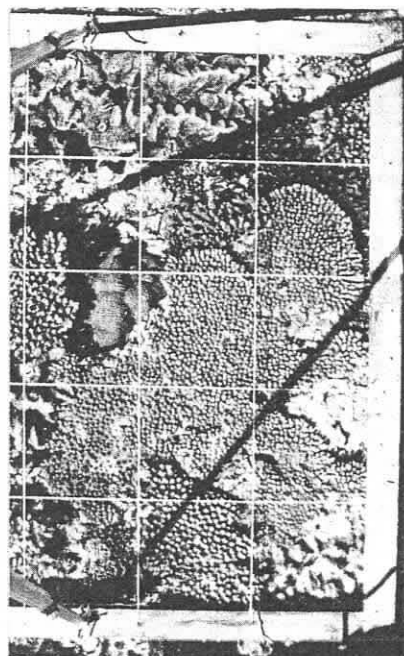
1963   1965

5

4

3

2

1

A   B   C   A   B   C

5

4

3

2

1
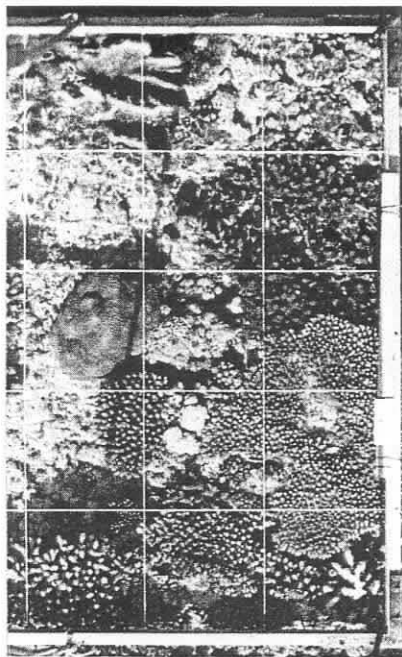
1969   1971

exist at equilibrium on a single hectare, or 10 species of corals on a single square metre. Whereas animals may specialize in feeding on certain prey (e.g. herbivorous insects on host plants, etc.), plants and sessile marine invertebrates have less opportunity for such fine specializations. Besides the well-known adaptations to different light intensities, associations between tropical trees and broad soil variations (parent material, drainage, etc.) or topography (tip-up mounds at the roots of fallen trees, ridges vs. slopes and stream courses, etc.) have been found (Richards 1952; Whitmore 1975; Williams *et al*. 1969; Austin, Ashton & Grieg-Smith 1972). Likewise, coral species show associations with broad zones such as reef flats, crests and with depth on outer slopes. However, none of these specializations seems sufficiently narrow to account for the high diversity shown. In addition, the individuals of different species are often intermingled in a complex pattern; if each species were highly specialized to habitat variation, this would require the environment to vary in a complex mosaic on a very small scale.

DISCUSSION: DIVERSITY AND EQUILIBRIUM

Environmental heterogeneity within a site will permit co-existence of different species, but probably not to the degree seen in tropical rain forests and coral reefs. With no disturbances beyond the death of individual trees and of coral colonies, further diversity requires that the system be open, in the sense of being subdivided into cells connected by migration of propagules, predators, etc. Then mechanisms such as circular networks or frequency-dependent mortality caused by physical damage or by natural enemies, either specialists or generalists that 'switch', may maintain co-existence of more species in either an equilibrium or non-equilibrium state (Table 7.1, step 3).

In the corals, circular networks were looked for but not found; competitive interactions were hierarchical, not circular (Connell 1976). Frequency-dependent mortality caused by natural enemies apparently does not occur; the starfish *Acanthaster planci*, one of the most effective predators on corals, attacked the rare species preferentially in the two studies where the relevant data were collected (Branham *et al*. 1971; Glynn 1974). In certain habitats (such as the reef crest at Heron Island), physical extremes caused proportionately more mortality in species that had been demonstrated to be superior competitors. Such mortality, though not necessarily frequency-dependent, will certainly promote co-existence in an open equilibrium.

However, in the tropical trees where frequency-dependent mortality has been looked for, it has been demonstrated for only a few species. All the experiments done and observations made in tropical forests pertinent to this subject are given in Tables 7.3 and 7.4. They involved species with large seeds, a trait of shade-tolerant, late-colonizing 'climax' species. The data show that within

the set of possible climax species most do not suffer frequency-dependent mortality and, as in corals, circular networks seems unlikely.

Thus, 'compensatory' mortality (Connell 1978) does not seem to be important in the tropical rain forests studied, and only in particular circumstances (reef crests) on coral reefs. One would then predict that, within a particular habitat, the one most effective competitor should eliminate all others as in step 4 of Table 7.1. Therefore, the principal way that high local diversity will be maintained is by a regime of sporadic disturbances that cause gaps into which different species invade, as shown by the regimes I and II of Table 7.1. This process can occur in several ways. The first, which I have called the 'Equal Chance' hypothesis (Connell 1978), would apply if all the species were equal in their abilities to disperse to a gap, become established and hold the space against further invasion. Aubreville's (1938) 'Mosaic Theory of Regeneration' was essentially this hypothesis, applied to a rain forest in Ivory Coast. The problem with it is that species need to be identical in their rates of increase and abilities to compete for sites. It seems unlikely that different species will be so alike or so precisely balanced for this hypothesis to apply.

The second way is that species may be adapted to occupy gaps of different sizes or at different times after they are formed. Grubb (1977) has called this sort of adaptation the 'regeneration niche'. Classes A, B and C in Table 7.1 represent three points in a continuum of sizes and/or times. If moderate to large-size gaps are formed regularly, this could remain an open non-equilibrium system of early- and intermediate-colonizing species (regime I). If, on the other hand, there is a long period without further disturbances, the succession of species represents an open non-equilibrium system, gradually becoming closed to earlier colonists as succession proceeds (step 2, Table 7.1).

Third, co-existence of competitors may be enhanced if disturbances happen frequently, even if the species are not equal so that some are always eliminated in competition within a cell, and even if there is no heterogeneity in the cells. In Caswell's (1978) model, co-existence of competitors in an open non-equilibrium system was prolonged if both the number of cells and the degree of 'connectedness' were increased. In forests or reefs, the number of empty cells increases if the disturbances cause only local damage (small gaps) and occur frequently. Connectedness increases with the degree of migration of propagules (seeds or larvae) between gaps. Co-existence in Caswell's (1978) model was prolonged when the migration rate of the inferior competitor was increased and when the rate of formation of new empty cells was raised by faster dispersal of a predator between cells. However, in forests or reefs, the dominant life forms (trees or corals) are immune to very small disturbances, in contrast to the more vulnerable annual herbs or algae. This puts a limit on the number of new empty cells that can be produced in these communities.

In summary, the species richness will be greatest if the disturbance regime is intermediate in both frequency and size of gaps formed, or if the site is near

the midpoint in a succession. Such gaps are certainly common in the tropics, produced by lightning strikes, wind storms, landslips, attacks by boring organisms in corals (Connell 1973), predators, etc. Shifting cultivation by low-density human populations is also an intermediate disturbance of significance in tropical rain forests. Since tropical rain forest trees and reef-building corals often occur at high diversity, and since compensatory mechanisms do not seem to play a significant role in the stands studied, it seems clear that regimes of 'intermediate disturbances' probably account for much of their diversity.

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